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Research Article

The contemporary records of aquatic plants invasion through the Danubian floodplain corridor in Serbia

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Abstract

Aquatic ecosystems are particularly vulnerable to introductions of non-indigenous species, which potentially lead to major disruptions in the functioning of these invaluable habitats. Despite the significance of aquatic systems, there is no collated data available on the aquatic non-native plants in Serbia. Consequently, the aim of this paper is to provide a first overview of the aquatic alien plant species recorded in Serbia, their origins, current distribution, habitat preferences and invasiveness status. This study comprises the results of a comprehensive literature review and extensive field research on lake and river systems over a nine year period (2007–2015), with the addition of data from the IASV database and Joint Danube Surveys 2 & 3. The results of this study show the presence of seven non-indigenous aquatic plant species in Serbia which, despite being a relatively low number when compared to France and Germany, is in line with most of the countries of the region (e.g. Croatia, Bulgaria and FYR Macedonia). The majority of the species are native to the Americas, which concurs with the results of previous studies at the European level, with only one species of Asian origin. The most abundant of the registered non-natives is *Vallisneria spiralis*, followed by *Azolla filiculoides* and *Elodea nuttallii*, while *Cabomba caroliniana*, as the newest registered aquatic alien in Serbia, has the least number of records. All of the registered non-natives predominantly occur in running waters, including as much as 91% of the records for *Elodea canadensis* and 85% for *Elodea nuttalli*. *Vallisneria spiralis* is present in five different EUNIS habitat types, while *Paspalum distichum* was recorded predominantly along the River Danube, thereby highlighting it as *P. distichum*'s main corridor of spread in Serbia. The distribution of all the recorded non-indigenous species is primarily linked to the northern, low-lying part of Serbia—i.e. Vojvodina Province. Such a distribution pattern is concordant with the presence of adequate habitat types, the courses of potential international invasion corridors in the Sava and Danube rivers and the position of the elaborate irrigation canal network of the Danube-Tisa-Danube Hydrosystem; but also with the frequency of studies carried out in this region over the years. Of the seven aquatic aliens present in Serbian waterbodies, three are considered to be highly invasive and one potentially invasive, while two have also been included in the list of 150 most widespread alien species in Europe.

Key words: macrophytes, non-native, rivers, lakes, EUNIS habitats, Middle Danube Basin

Introduction

Biological invasions are a phenomenon threatening biodiversity worldwide (Vilà et al. 2007; Catford et al. 2012; Roy et al. 2014). However, certain habitats like urban areas, riparian zones and freshwater ecosystems (Sala et al. 2000; Vilà et al. 2007; Chytrý et al. 2008a, b; Coetzee et al. 2009; Chytrý et al. 2009; Pyšek et al. 2010), with fluctuating availability of resources and high propagule pressure, are more vulnerable to invasion by alien species than others (Chytrý et al. 2008a, b; Pyšek et al. 2010).

Aquatic freshwater ecosystems are especially prone to invasions by alien species (Coetzee et al. 2009), when compared to terrestrial ecosystems (Sala et al. 2000). A steady rise in the number of introductions of new aquatic non-native species has been recorded in Europe, particularly over the past 60 years (Nunes et al. 2015). Rivers, streams and canals act as perfect routes linking neighboring habitats, thus enabling the rapid dispersal of propagules of alien species (Lodge et al. 1998; Rahel and Olden 2008). Furthermore, as these systems are often under strong anthropogenic influence (Dudgeon et al. 2006;

Strayer and Dudgeon 2010), this highlights the role that human activities have as a major source of the introduction and spread of aquatic invaders (Loo et al. 2007).

Aquatic invaders present a serious threat for the functioning and management of aquatic freshwater ecosystems (Thum and Lennon 2010), leading to losses in biodiversity; disruption of natural flow dynamics; degradation of water quality (see Stiers et al. 2011); changes in soil properties (Windham and Lathrop 1999) and biogeochemical functions (Ravit et al. 2003); and disturbances to recreational activities, e.g. boating, swimming and fishing (Thum and Lennon 2010). Moreover, the economic costs of control of aquatic invasive plant species are high (Pimentel et al. 2000, 2005). In Spain the cost of control and eradication of *Azolla filiculoides* is estimated to be €1 million per year and that of *Eichhornia crassipes* ((Mart.) Solms, 1883) is €3.35 million per year (Andreu et al. 2009), while the cost of *Hydrilla verticilata* (L.f.) Royle 1839 control in the state of Florida reaches up to $14.5 million per year (Coetzee et al. 2009).

Hussner (2012) highlights the need to consider the majority of more than 400 alien aquatic and semi-aquatic plant species, which are currently being traded across Europe (Hussner 2008), as potentially invasive in European freshwater habitats. Given this, and as a consequence of the numerous negative effects that alien plant species have on aquatic habitats and their functionality, there have been a number of papers dealing with the issue of aquatic alien plant species on a national level (e.g. Alexandrov et al. 2007; Anastasiu et al. 2007; Thiébaut 2007; Hussner et al. 2010; Tosheva and Traykov 2010, 2013; Wang et al. 2016). However, there is a general lack of data for alien and invasive species in Serbia, both in online databases—DAISIE (http://www.europe-aliens.org), NOBANIS (http://www.nobanis.org), EPPO (http://www.eppo.int) and the Invasive Species Specialist Group (http://www.issg.org), and in the peer reviewed literature, with the exception of a few chosen publications (e.g. Vrbničanin et al. 2004; Vukov et al. 2008, 2013; Šilc et al. 2009, 2012; Lazarević et al. 2012; Anačkov et al. 2013; Anđelković et al. 2013; Glišić et al. 2014), dealing with a specific set of species and/or habitats. As a result, this region is often shown as not having any invasive species—a blank spot on the European map of alien invasive species (e.g. Figure 3 in Chytrý et al. 2009 and Figure 1 in Lambdon et al. 2008). This paper therefore aims to present a first study of the aquatic alien plant species present in the freshwaters of Serbia.

Material and methods

Definitions

This paper follows the distinction between alien and native species as presented by Pyšek et al. (2004), considering as alien those plant species "whose presence in a given area is due to intentional or unintentional human involvement, or which have arrived there without the help of people from an area in which they are alien", while a neophyte is regarded as an alien species introduced after the year 1492 (see Richardson et al. 2000).

All those plant species that are closely bound by at least one part of their life cycle to aquatic habitats were considered as relevant. However, unlike Hussner (2012) who has excluded from his research those species that also grow in habitats other than the aquatic, this paper includes *Paspalum distichum* L., 1759 (syn. *Paspalum paspalodes* (Michaux) Scribner, 1894) in the results, as it is a non-submerged aquatic plant, which often occurs in streams and alluvial flatlands worldwide, and is considered to be among the most successful invasive species of aquatic and riparian areas (see Aguiar et al. 2005).

The nomenclature of the species follows the ITIS database (ITIS 2015), with the exception of *Azolla* species, which are regarded as separate species, concurring with the Flora of North America (Lumpkin 1993), The Plant List (http://www.theplantlist.org/tpl1.1/search?q=Azolla) and the Catalogue of Life entries (Hassler 2016), as well as a study by Pereira et al. (2011).

Habitat data was recorded following the national system for the classification of habitats (Lakušić and Medarević 2010), and later adapted to comply with the EUNIS system (European Union Nature Information System, Davies et al. 2004). EUNIS classification was chosen as it presents a comprehensive framework for the classification of European habitats, and provides detailed descriptions of its habitat types. The aim of the EUNIS habitat classification is to present researchers in Europe with a common reference set of habitat types, which allows for habitat data to be reported in a comparable manner (Davies and Moss 2002). One of the greatest values of the EUNIS habitat classification is its comprehensive nature, as it covers the entire area of the European mainland and sea (Davies et al. 2004). The EUNIS system has six hierarchical levels ranging from 1 to 6, where level 1 is the highest habitat rank and includes 10 habitat categories. The habitat types are described using a set of parameters and the hierarchy of the system is achieved through the application of parameter-based criteria, in the form of keys for the identification of habitats, in a manner similar to species identification keys (Moss 2008). Habitat type C (EUNIS Level 1) encompasses all inland surface waters, i.e. the "non-coastal, above-ground open fresh or brackish waterbodies", including their littoral zones, which are flooded "frequently enough to prevent the formation of closed terrestrial vegetation" (Davies et al. 2004). Habitat types C1, C2 and C3 (Level 2) represent all surface standing waters, surface running waters and littoral zones (e.g. reedbeds and other water-fringing vegetation) of inland surface waterbodies, respectively. The results were analyzed to Level 3 of the EUNIS classification, i.e. surface standing water habitat types, representing mesotrophic (C1.2) and eutrophic (C1.3) lakes, ponds and pools and temporary lakes, including ponds and pools, of the C1.6 habitat type; surface running waters, encompassing slow-flowing watercourses (C2.3) and tidal rivers (C2.4); and littoral zone habitats, which include water-fringing reedbeds (C3.2) and species-poor beds of low-growing water-fringing or amphibious vegetation (C3.4). The detailed descriptions of Level 3 categories which were included in the analysis (Figure 3) can be found in Davies et al. (2004).

Data collection

This paper combines the results of a detailed review of the available literature (e.g. Babić 1971; Radulović 2000, 2005; Stevanović et al. 2003; Panjković 2005; Polić 2006; Lazić 2006; Nikolić et al. 2007, 2009, 2011, 2014; Vukov 2008; Vukov et al. 2008, 2013; Stojanović et al. 2009; Ljevnaić-Mašić 2010; Radulović et al. 2011, 2012; Laketić 2013; Laketić et al. 2013), with the addition of data from the Invasive Alien Species of Vojvodina database (IASV 2011) and results obtained through extensive field research done over the past 7 years. A search of the relevant herbaria collections (BEO, BEOU, BUNS) was also conducted. However, these results were excluded from the paper as: 1) the number of herbaria records was significantly lower than other sources, because our target species are aquatic and were rarely collected for herbaria collections; and 2) these records were often of insufficient geographic precision for them to be georeferenced using OziExplorer software, and contained little to no data on the habitat type or plant community. Data pertaining to the Danube river basin have been expanded by the addition of the records acquired during the Joint Danube Survey 2 (ICPDR 2008) and Joint Danube Survey 3 (ICPDR 2015), obtained within the framework of the European project "SOLUTIONS For Present and Future Emerging Pollutants in Land and Water Resources Management".

Field research

Field observations were carried out across Serbia over nine years, from 2007 to 2015, and included both river and lake systems. Field research for the vegetation of standing waters was performed during the summer months of 2007–2011 (Radulović et al. 2011; Laketić 2013; Laketić et al. 2013), while the extensive research for the vegetation occurring along Serbian rivers was carried out during the summer months of 2010–2015. For the river systems, sampling followed the standard River LEAFPACS methodology (Willby et al. 2012) used to assess river macrophytes (CEN 2003), while for lakes the standard LEAFPACS field protocol (Willby et al. 2009), was used in accordance with the Pan-European standard for the sampling of the macrophyte vegetation in lakes (CEN 2007). Sampling quadrats (1–9 m^2 depending on vegetation type), were set along 100 m length sectors (stretches). Each 100 m sector was divided into 5 sub-sectors at 20 m intervals. Samples were taken within every sub-sector at 0.25, 0.5, 0.75 and >0.75 m water depth. The number and locations of sectors depended on the heterogeneity of the vegetation (Gunn et al. 2010).

For lakes, the sampling points were located within each of the main vegetation types (Willby et al. 2009). From the mid-point of the 100 m sector a boat transect was set up perpendicular to the lake shore. A series of sample points were surveyed at 0.5 m depth intervals, between the end of the transect and the shoreline marker. At each sample point, all aquatic macrophyte species were recorded using a combination of bathyscope and grapnel sampling.

For rivers, vegetation data were collected along longitudinal 100 m river stretches, with an average distance of 500 m between two stretches, depending of the length of the river (Willby et al. 2012). At each river stretch, the presence and a visual estimate of the percentage of the river channel covered by each of the macrophyte taxa were recorded (Dawson et. al. 1999; Holmes et al. 1999). The collected plant material was subsequently identified according to Tutin et al. (1964, 1968, 1972, 1976, 1980), Sarić (1992), and Javorka and Csapody (1975). The collected specimens are deposited in the BUNS Herbarium, University of Novi Sad.

Data analysis

The georeferencing of historical data on species distribution was carried out using the OziExplorer software (OziExplorer 2009), while the field records were obtained using a GPS Garmin eTrex 10 hand-held GPS navigator. Distribution maps were based

Table 1. List of registered aquatic alien plant species in Serbia.

	Taxon	Family	Growth form*	Native area	Number of records
1	*Azolla caroliniana* Willdenow 1810	Azollaceae	er nat Hyd T	N, S, C America	42
2	*Azolla filiculoides* Lamarck, 1783	Azollaceae	er nat Hyd T	N, S, C America	69
3	*Cabomba caroliniana* A. Gray, 1837	Cabombaceae	rhiz sbm Hyd G	S America	4
4	*Elodea canadensis* Michaux, 1803	Hydrocharitaceae	er sbm Hyd G	N America	46
5	*Elodea nuttallii* (Planch.) H. St. John, 1920	Hydrocharitaceae	er sbm Hyd G	N America	54
6	*Paspalum distichum* Linnaeus, 1759	Poaceae	stl emer Hyd G	S, C America	19
7	*Vallisneria spiralis* Linnaeus, 1753	Hydrocharitaceae	rhiz sbm Hyd G	N Africa, Asia, S Europe	88

* er – erantus (hovering) , nat – natans (floating), rhiz – rhizomatous (plants with a rhizome) , sbm – submersum (submerged), Hyd T – Hydro Terophyta, Hyd G – Hydro Geophyta.

on the geographic data (listed in supplementary Tables S1–6) resulting from the literature survey, invasive species database and field observations, and were constructed using the free DIVA-GIS 5.2 software (Hijmans et al. 2004) in the UTM projection (WGS84 elipsoid).

A problem with the verification of data pertaining to *Azolla* species must be highlighted. In Serbia it has long been accepted that only one species, *Azolla filiculoides* Lamarck 1783, is present in the aquatic systems. This is concurrent with the findings of Pyšek et al. (2012), who state that *A. filiculoides* is the *Azolla* species most widely present in Europe, while *Azolla cristata* Kaulf. 1824 has only been recorded in the Netherlands. However, several literature sources cite *A. caroliniana* as also being present in Serbian waterbodies. Although this could have resulted from imprecise taxon identification of *A. filiculoides*, this cannot be claimed *a priori*, and as they have been published as such, we have been obliged to include them in our results. There are many unresolved issues pertaining to these two species worldwide, and some long-standing controversies have ensued over the taxonomy of the *Azolla* species (Pyšek et al. 2012). On the one hand, the research of Evrard and van Hove (2004) has shown that only two species of *Azolla* can be taxonomically differentiated in America, placing the type specimen of *Azolla caroliniana* Wildenow 1810 into what is known as *A. filiculoides*. The same is true of the ITIS database (ITIS 2015). However, in this paper, we have treated them as two separate species, which concurs both with the Flora of North America (Lumpkin 1993), The Plant List (http://www.theplantlist.org/tpl1.1/search?q=Azolla), the Catalogue of Life entry (Hassler 2016) and a more recent study by Pereira et al. (2011), which, by combining morphological and molecular characters, has given us new insights into the taxonomy of *Azolla* species. The research of Pereira et al. (2011) has positioned *A. caroliniana* into a single subcluster, thereby separating it from *A. filiculoides* and confirming its clear taxonomic position as an accepted species.

The general tendencies and relative abundance of alien species with regards to their geographic origin, habitat preferences and overall distribution are presented. The area of origin of species was delineated based on the data from the available literature (see References). Life forms of each species are given according to the revised and updated (Stevanović 1992) classification of Ellenberg and Muller-Dambois (1967). When considering the area of geographical origin, those species which originate from two different continents were regarded as representatives for both of them.

Results and discussion

Based on the literature and field data collected, seven alien aquatic plant species have been documented in the freshwaters—rivers, lakes and canals—of Serbia (Table 1). All of the recorded species are considered to be neophytes (see Pyšek et al. 2012).

The number of aquatic aliens is relatively low when compared to some European countries like France, which has the highest number of documented aquatic aliens in Europe (31 species, Thiébaut 2007), and Germany (24 species, Hussner et al. 2010). However, in comparison with other countries of the region, e.g. Bulgaria and FYR Macedonia which have 9 and 4 non-indigenous aquatic species respectively (see Hussner 2012; but also counting *P. distichum*) and Croatia, which has 6 (Nikolić 2015), numbers are comparable. Nevertheless, as the neighboring country of Romania has 13 aquatic aliens (Anastasiu et al. 2007) and Hungary 26 (Mesterházy et al. 2009), it can be expected that the number of aliens in Serbia has the potential to increase, especially considering that

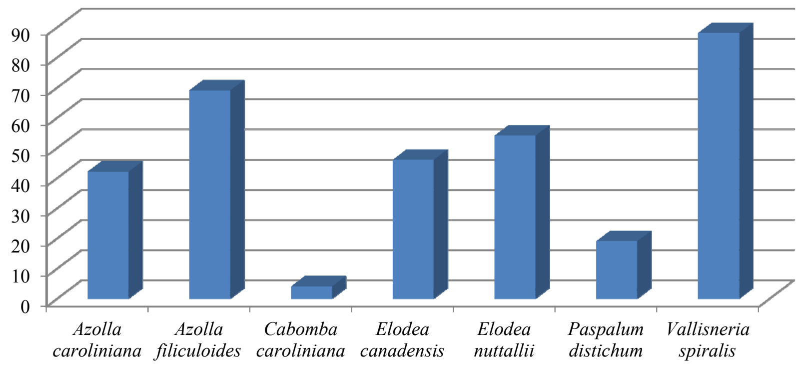

Figure 1. Number of records of alien invasive aquatic species in Serbia.

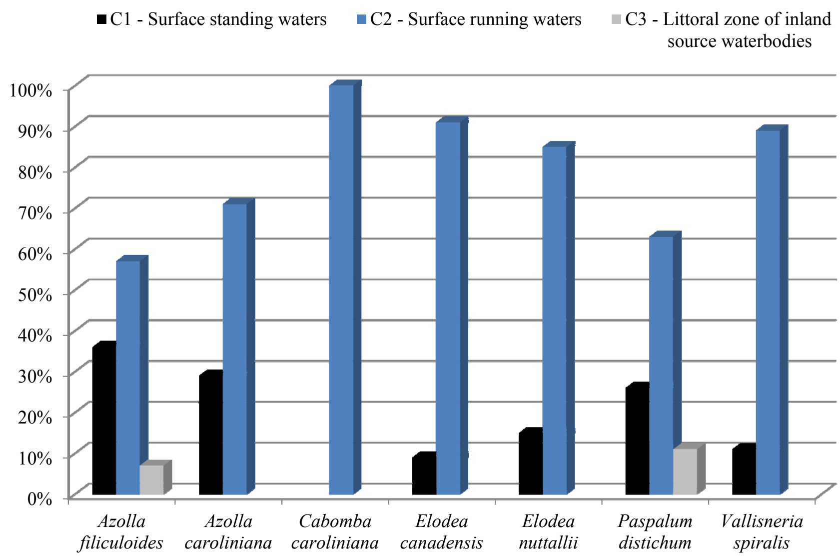

Figure 2. Proportion of records of aquatic alien species in different habitat types (EUNIS classification).

that Serbia borders with Romania and Hungary, and shares a number of watercourses with them.

Vallisneria spiralis is the most abundant of the recorded species, with 88 records. The second most recorded is *A. filiculoides* (69 records), closely followed by *Elodea nuttallii,* with 54 records. *P. distichum* and *Cabomba caroliniana* are the least numerous of the registered aliens, with only 19 and 4 records respectively (Figure 1).

There is a clearly evident trend for all species to be dominant in running waters rather than standing waters (Figure 2). Hussner et al. (2010) state that the introduction of alien aquatic plant species mostly occurs through the aquarium trade or the release of ship ballast waters. Additionally, the authors name pleasure boats, ships (Leung et al. 2006) and fish stocking (Pollux et al. 2006) as other important potential vectors of aquatic aliens. Furthermore, rivers and canals act as corridors connecting neighboring habitats, thus facilitating the dispersal of alien species' propagules (Lodge et al. 1998; Rahel and Olden 2008). These features of running water systems (i.e. rivers, streams, canals) could explain the discrepancy in the proportion of aquatic aliens present in running *vs.* standing waters in Serbia (Figure 2).

Places of origin of the aquatic alien plants

Table 1 gives an overview of the origin of the registered aquatic alien plant species in Serbia, with 57% of the species being native to both North and South America. Thus, the majority of alien aquatic species in Serbia are native to Americas, while Asia and Northern Africa are both represented by just one species (Table 1). These results concur with those for Germany (Hussner et al. 2010), and Europe in general (Hussner 2012), in which most alien aquatic plants are native to North and South America.

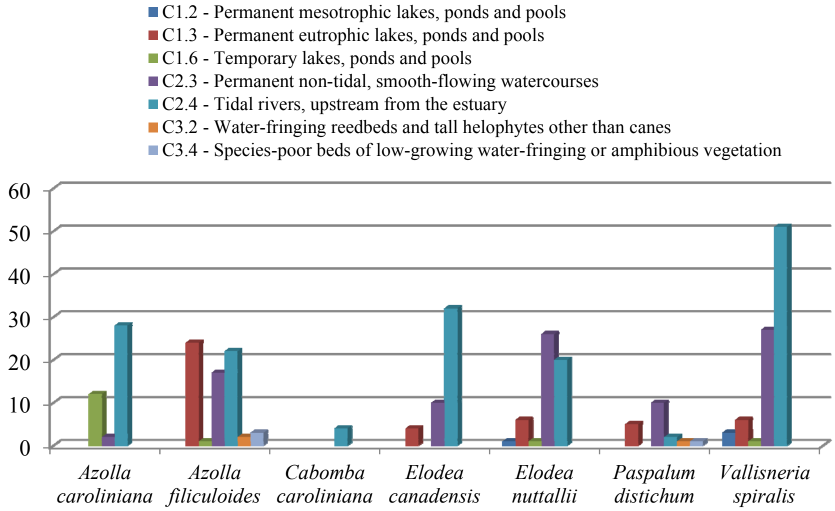

Figure 3. The number of records of aquatic alien plant species in different EUNIS habitat types.

However, although Hussner (2012) suggests that in European freshwater systems there is an ongoing trend for an increase in the proportion of alien species originating from Asia, for now there is just one species of Asian origin registered in Serbia (*V. spiralis*, Table 1).

Distribution of aquatic alien plants species within Serbia

Elodea spp. are submerged perennial species, with underwater leaves and floating flowers, which are usually rooted in mud (Bowmer et al. 1995). They are found predominantly in meso- and eutrophic waters, where they exhibit high growth rates, tolerating a wide range of environmental conditions (Erhard and Gross 2006). As there is no seed production in *Elodea* ssp. in their introduced range, their reproduction and spread is limited to asexual propagules (Redekop et al. 2016). Dispersal is predominately by means of their vegetative parts (Barrat-Segretain and Cellot 2007), mainly stem fragments (Barrat-Segretain and Elger 2004).

Elodea canadensis and *E. nuttallii* were introduced into Europe in the 19th and 20th century, respectively. They have been spreading across Europe ever since (Barrat-Segretain et al. 2002; Barrat-Segretain and Elger 2004), reaching high densities and forming dominant monospecific stands (Erhard and Gross 2006). There have also been some indications that allelopathic interactions of these species could affect the development of other aquatic primary producers (Erhard and Gross 2006). *Elodea nuttallii* has been replacing *E. canadensis* in many sites across Europe (Simpson 1984; Barrat-Segretain 2001). Recent studies have shown that vegetative fragments of *E. nuttallii* have higher dessication resistance than those of *E. canadensis* (Barrat-Segretain and Cellot 2007). Furthermore, comparison of their life histories has shown that *E. nuttallii* has a higher growth rate and lower sensitivity to light intensity decreases than *E. canadensis* (Barrat-Segretain 2004; Barrat-Segretain and Elger 2004) which could, coupled with the higher regeneration and colonization ability of its vegetative fragments, account for the better competitive success of *E. nuttallii* over *E. canadensis* (Simpson 1990).

Although *E. nuttallii* and *E. canadensis* are among the most common species in the lakes of north-western Europe (Hilt and Gross 2008), most of the records of these species in our country (Figure 3) have been documented in surface running waters: for *E. canadensis* 91% of the records (10 records in C2.3 EUNIS category – Permanent non-tidal, smooth-flowing watercourses and 32 records in C2.4 – Tidal rivers, upstream from the estuary, Figure 3) and for *E. nuttallii* 85% (26 records in C2.3 and 20 records in C2.4, Figure 3).

With regards to their geographic distribution, *Elodea* species are mostly found within the northern province of Vojvodina and along the Danube, with the exception of a single record for each located in the southern part of Serbia—Nišava river for *E. canadensis* and Vlasina Lake for *E. nuttallii* (Figures 4 and 5). While *E. canadensis* mostly occurs in different sections of the main network of irrigation canals of Vojvodina, evident both from the results of its distribution (Figure 3) and the distribution map

(Figure 4), *E. nuttallii*, although also present in the waters of the network of canals (37% of the records, Figure 3), is mostly distributed along the Danube (48% of the records, Figure 3) and in its littoral zones, as clearly seen from the map of its distribution (Figure 5).

Azolla species are floating heterosporous ferns, which are native to the Americas and invasive in many other parts of the world (Murillo et al. 2007), with *Azolla filiculoides* spreading across nearly the entire European continent (Szczęśniak et al. 2011). *Azolla* spp. rarely float as individual plants, but as mats, which can be very dense and up to 20 cm thick (McConnachie et al. 2003), thus affecting entire ecosystems and all features of water exploitation (Van Wilgen et al. 2001). They are mostly found in ponds, ditches, water reservoirs and slow flowing rivers and canals (Szczęśniak et al. 2011). A very high growth rate is characteristic: in ideal conditions they are capable of achieving a doubling time of only four to five days, and a daily rate of increase of over 15% (Murillo et al. 2007). *Azolla* spp. reproduce both sexually (via spores) and asexually, by undergoing rapid vegetative reproduction through the fragmentation of rhizomes. The rhizomes of these species are very fragile, causing them to easily break into small fragments. The dispersal of such small rhizome fragments is the main mechanism of dispersal of these species in their introduced range. However, although the most important factors in their dispersal in Europe are human activities, both intentional and unintentional, natural dispersal vectors (e.g. waterbirds, Hussner and Lösch 2005), and anemo- and hydrochory also play a significant role in furthering their spread (Szczęśniak et al. 2011).

Azolla filiculoides, the second most abundant species, is present in all three types of inland surface water habitats. Its records are mostly distributed in surface running waters (C2 EUNIS habitat types), with 57% of the records (39 records, Figure 3). Twenty five records (36%) are related to surface standing waters (C1 habitat types) and 5 to the littoral zone of inland surface waterbodies (7%). Of the data for the running waters, 25% of the overall records are for permanent non-tidal, smooth-flowing watercourses (C2.3) and 32% for tidal rivers, upstream from the estuary (C2.4) (Figure 3).

Although the number of records for *A. caroliniana* overall is smaller than for *A. filiculoides* (42 to 69), *A. caroliniana* is also mostly distributed in surface running waters, with 71% (30 records) of the records. However, unlike *A. filiculoides*, *A. caroliniana* has only been recorded twice in permanent smooth-flowing watercourses, while it is mostly present in the C2.4 habitat type (67% of the records, Figure 3).

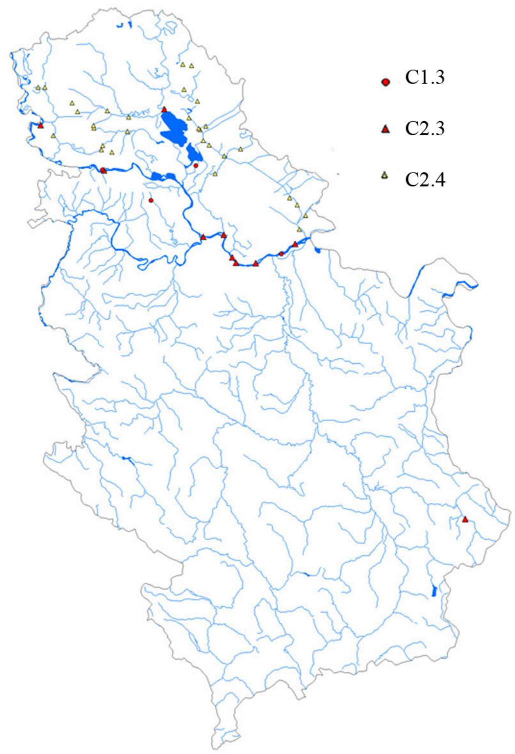

Figure 4. Geographic distribution of *Elodea canadensis* in Serbia.

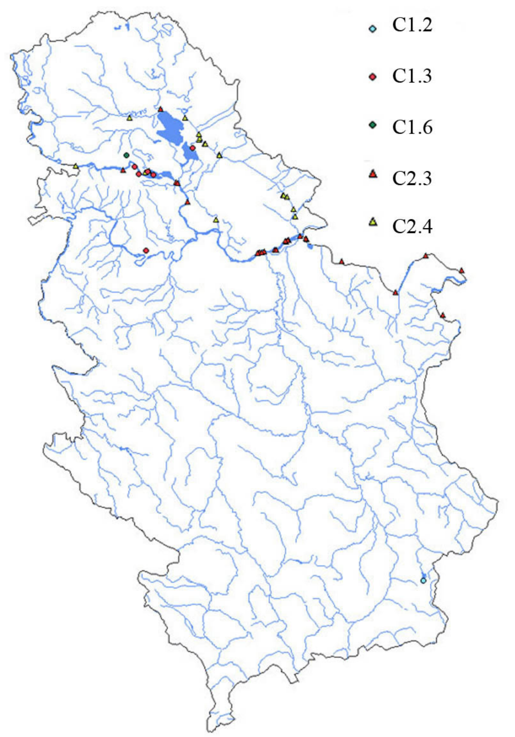

Figure 5. Geographic distribution of *Elodea nuttallii* in Serbia.

The records for *A. caroliniana* could have resulted from a misidentification of *A. filiculoides*, as explained previously, in which case all of the records pertaining to *Azolla* species are actually the results for the distribution of *A. filiculoides*.

All the records of *A. caroliniana* in Serbia are located north of the Sava and Danube rivers, i.e. in the northern province of Vojvodina (Figure 6). The same tendency is evident for *A. filiculoides*. However, this species also has a number of records registered along, and within the oxbows of the River Danube, spreading all the way to the country's eastern border with Bulgaria (Figure 7). In addition, *A. filiculoides* is often found within the main irrigation canal network of Vojvodina and along its highly regulated waterbodies, which concurs with the results presented in Figure 3.

Vallisneria spiralis, commonly known as tapegrass or eelgrass, is a rhizomatous submerged perennial macrophyte, with fibrous roots, a short stem and horizontal stolons (Collas et al. 2012). It can grow in still, but also slow and fast running waters, on muddy, sandy and gravelly substrates (Hussner and Lösch 2005). It forms plagiotropic stolons, which spread horizontally above the substrate surface, forming a number of ramets at its nodes. Those ramets form a large clonal system, being interconnected through the stolons (Xiao et al. 2006), and enable this plant to grow underneath the canopy of other aquatic plants (Xiao et al. 2007). The most common means of its propagation is asexually, through stem fragmentation (Madsen and Smith 1997) and via the stolons (Hutorowicz and Hutorowicz 2008), which can lead to the development of very dense stands, often formed in the littoral zones of ponds and lakes (Collas et al. 2012).

Vallisneria spiralis is generally seen as a typical and valuable component of eutrophic lowland water ecosystems (Sand-Jensen et al. 2008), where it improves the stability of the sediment and influences the biogeochemistry of the ecosystem as a whole (Bolpagni et al. 2015). However, it is considered to be one of the most widely distributed aquatic alien weeds in both Central and Northern Europe (Hussner 2012). This species is also characterized by high ecological plasticity and could prove to be a potential competitor of native macrophytes in oligotrophic waters of moderate elevations, where it has been shown to exhibit "pioneering behavior" (Bolpagni et al. 2015). As the most abundant of the species registered in our country, *V. spiralis* was present in five different EUNIS habitat types, with the majority of the results (57%) recorded in tidal rivers (C2.4 EUNIS habitat type). A significant number of records (31%) were also registered in permanent non-tidal,

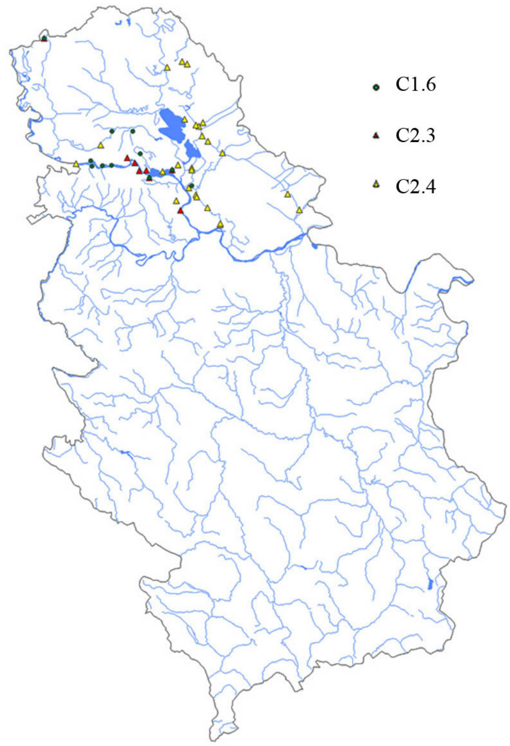

Figure 6. Geographic distribution of *Azolla caroliniana* in Serbia.

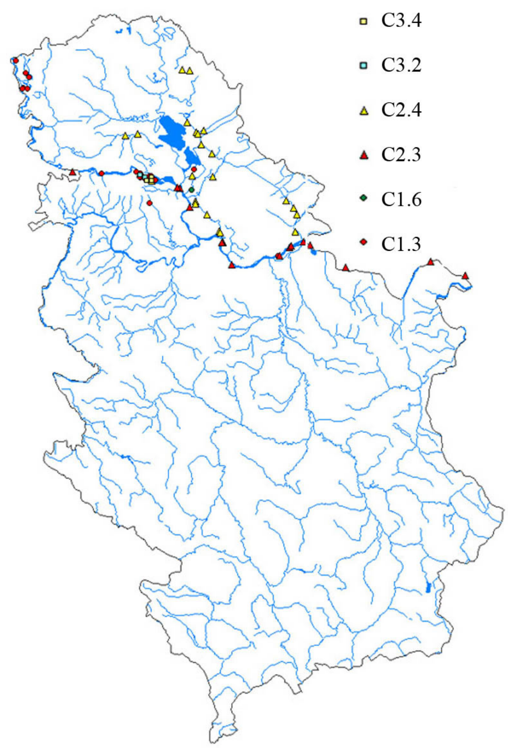

Figure 7. Geographic distribution of *Azolla filiculoides* in Serbia.

smooth flowing watercourses (C2.3 in the EUNIS habitat classification, Figure 3).

The distribution map of *V. spiralis* (Figure 8) shows that this species presence has also been recorded in locations other than the northern province of Vojvodina. Two of these records coincide with mesotrophic lakes—one each in Eastern (Grliško Lake) and Western Serbia (Spajići Lake), and others with surface running waters (rivers Toplica, Nišava, Mlava and Crni Timok) of Eastern and Southeastern Serbia.

Paspalum distichum, commonly known as knotgrass, is a species originating from the tropical areas of America, where it is even considered to be a desirable element of ecosystems (Aguiar et al. 2005). On the other hand, in habitats where it has been introduced, *P. distichum* frequently forms dense monospecific stands on stream banks and in riparian zones, suppressing the native vegetation (Aguiar et al. 2005). *Paspalum distichum* is a perennial species, with creeping, highly branched rhizomes and stolons, which create expansive mats (DiTomaso and Healy 2007). It can increase its invasion potential and colonize non-invaded areas through the dispersal of fragments of its rhizomes and stolons (Aguiar et al. 2005), which are carried by floodwaters, or moved as a result of soil disturbances, agricultural measures and other human activities (DiTomaso and Healy 2007). Furthermore, high numbers of visitors to riparian areas and the presence of human infrastructure in these zones also increase the spread of its propagules (Aguiar et al. 2005). *Paspalum distichum* was recorded for the first time in the territory of former Yugoslavia in the first half of the 20th century (Stevanović et al. 2004). In Serbia, the highest number of records (50%) occurred in non-tidal, smooth flowing rivers, i.e. C2.3 category, while 25% of the records were documented in tidal rivers (C2.4 habitat type, Figure 3). *Paspalum distichum* is present exclusively along the Danube and within its oxbows and meanders (Figure 9), which gives a strong indication as to its main corridor of spread. These results are in accordance with a previous study on its distribution (Stevanović et al. 2004), which recorded *P. distichum* over large areas along the 250 km long stretch of river Danube, from Belgrade to the Djerdap dam. This alien species is rapidly expanding, and colonizing new habitats, thereby excluding native macrophyte vegetation of *Potamogeton* and *Ceratophylum* species (Stevanović et al. 2004).

Cabomba caroliniana, more commonly known as fanwort, is a subtropical, freshwater, submerged, perennial species, native to South America (McCracken et al. 2013), which grows prolifically forming dense populations and has invaded and become naturalized

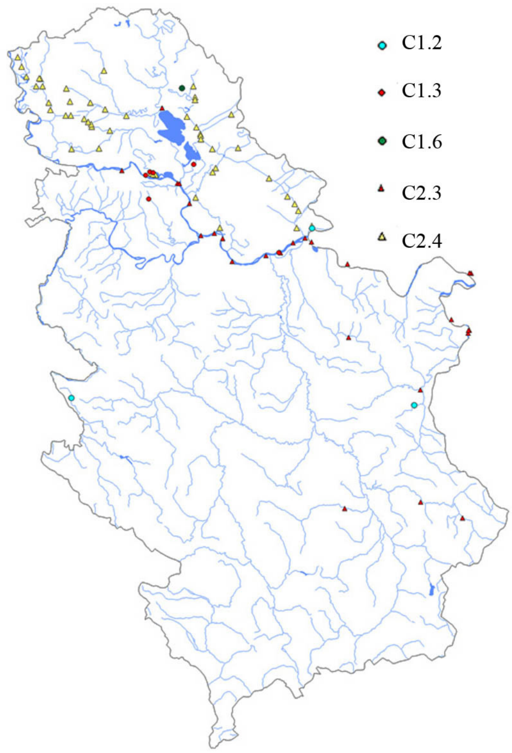

Figure 8. Distribution map of *Vallisneria spiralis* in Serbia.

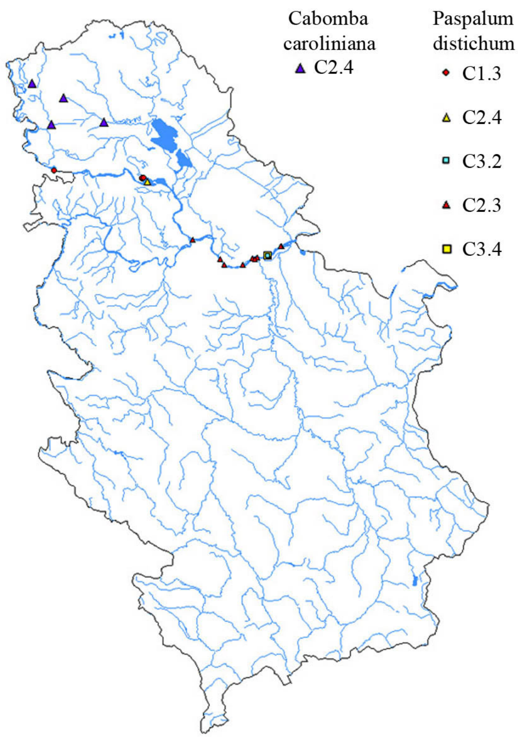

Figure 9. Distribution map of *Cabomba caroliniana* and *Paspalum distichum* in Serbia.

in many countries of the world (Hogsden et al. 2007). It grows in a wide range of conditions, both acidic and alkaline, and in stagnant and swiftly flowing freshwaters (Wilson et al. 2007; Jacobs and Macisaac 2009). Although it is mostly found in shallower waters (1–3 m depth), it has also been shown to grow in deeper water of up to 10 m (Hogsden et al. 2007; Wilson et al. 2007). It can reproduce both sexually (entomophily, Wilson et al. 2007) and asexually, by means of autofragmentation, under the condition that there is at least one node and leaf intact (Mackey and Swarbrick 1997). *Cabomba caroliniana* is an alien species which was registered in Serbia for the first time in 2008 (Vukov et al. 2013) in a Vrbas-Bezdan canal of the main irrigation canal network of Serbia. It was subsequently recorded in several new localities, all of them along the different sections of the canal network of the Hydrosystem Danube-Tisa-Danube, in Vojvodina Province (Figure 9). Therefore, all of the records of this species are connected to the C2.4 EUNIS habitat type. Vukov et al. (2013) have hypothesized that this invasive alien aquatic species has occurred in Serbia either as a result of anthropogenic factors (people disposing of aquarium plants) or as a result of its spread from the canal network in Hungary, where it has established overwintering populations over the last two decades (Mesterházy et al. 2009), highlighting that the second possibility is the more likely reason for its occurrence.

The distribution maps of all aquatic aliens registered in Serbia clearly show that the vast majority of records are primarily grouped in the northern, lowland part of Serbia—Vojvodina Province. There are a number of reasons which affect such a distribution of non-indigenous macrophytes in Serbia. First, the habitats in which these species are generally present, i.e. slow-flowing, regulated rivers and irrigation canals, are located in this region. Also, the watercourses of the Danube and Sava rivers, as potential international invasion corridors, are mostly found in this part of Serbia. Most aquatic invasions follow a west to east direction, thereby following the principal ship routes (Hussner et al. 2010), which may be another explanation for why the area of the Vojvodina Province, with its many navigable water courses, is most affected by the invasion of aquatic aliens. Where lakes are concerned, our findings concur with the results of Lacoul and Freedman (2006), which show that the richness of aquatic plant species in lakes has a negative relationship with altitude, as the majority of our records are found in the lakes of the northern, lowland part of Serbia. Lastly, the rivers and canals of this region have been studied more extensively and regularly over the years (see References), thereby providing us with a very thorough and detailed literature source. However, bearing in mind the location of favorable habitats and invasion corridors, there is no reason to suspect that the greater wealth of data available for Vojvodina Province has affected the overall validity of our results.

Invasiveness status of the registered aquatic aliens

Of the alien aquatic plant species recorded in Serbian waterbodies (Table 1), *E. canadensis, E. nuttalli* and *P. distichum* are listed as highly invasive and *A. filiculoides* as potentially invasive in the preliminary list of invasive plant species of Serbia (Lazarević et al. 2012), and all of them are included in the online database of invasive alien species of Vojvodina (IASV 2011). Also, *E. canadensis* and *A. filiculoides* are listed among the Europe's top 150 most widespread alien species (Lambdon et al. 2008). Furthermore, of the recorded species, EPPO (http://www.eppo.int/invasive_plants/ias_lists.htm) has put *C. caroliniana*, *E. nuttalli* and *P. distichum* on the List of invasive alien plants and *A. filiculoides* on the Observation list of invasive alien plants, therefore highlighting their potential harmful effects and possibility of further spread.

Implications for the Water Framework Directive

The biomonitoring of aquatic ecosystems in Europe has changed dramatically over the last fifteen years as a result of the requirements stipulated by the EU Water Framework Directive 2000/60/EC (WFD). This Directive has required assessment methods for different ecosystem types and different groups of organisms to be developed (Birk et al. 2012). As a result, a plethora of different country-specific methods has been developed across Europe, aimed at various combinations of water categories and groups of organisms (Birk et al. 2012). Although aquatic macrophytes constitute a significant structural element of aquatic ecosystems, often forming vast stands and therefore requiring large-scale surveys, as with the fish fauna, a small number of taxa of aquatic macrophytes are considered to be relevant for bioassessment within the framework of the WFD (Birk et al. 2012). A considerable drawback of the WFD is that, although it includes a number of different relevant parameters, invasive alien species have been overlooked, although they exert a significant pressure on aquatic ecosystems in the context of the objectives of the Directive (Cardoso and Free 2008; Vandekerkhove et al. 2013). Knowing that invasive alien species are able to modify the native biological structure and ecological functioning of the ecosystem, their assessment as a biological pressure should become an integral part of status assessments

(Cardoso and Free 2008). However, since 2002, when invasive alien species were officially acknowledged as a pressure by the WFD, only a few EU Member States have incorporated the pressures exerted by alien species in their WFD status assessments (Vandekerkhove et al. 2013). Vandekerkhove et al. (2013) highlighted that in recent years the efforts to correlate the pressures of invasive alien species with the ecological status of aquatic systems have either been restricted in geographical scale, or limited to single elements of biological quality. These authors identified 34 species of high impact which are associated with aquatic habitats. Out of the 17 most common high impact aquatic alien invasives, seven are strongly associated with a low status category of waterbodies. Among those seven species, three aquatic alien invasives were registered in this study in Serbia: *A. filiculoides*, *E. canadensis* and *E. nuttallii*.

Comparison with neighboring countries

All of the alien species recorded in Serbia are also present among the 13 aquatic alien species registered in Romania (Anastasiu et al. 2007). In Hungary, *E. canadensis* is mostly found in artificial standing waters, oxbow lakes and irrigation canals with slow-flowing water (Király et al. 2008), whereas in Serbia this species has been recorded mostly along the different sections of irrigation canals of the northern part of Serbia and is very rarely found in standing waters (only 9% of records, Figure 3). *Elodea nuttallii* has also become abundant in Hungary, primarily along the canals of the Danube plain, south of the capital. This distribution could be linked to its distribution in Serbia, and potentially points to one of the sources of its introduction, as in Serbia it is mostly found along the Danube (48% of the records, Figure 4). For Croatia, only *E. canadensis* and *P. distichum* are listed as invasive by some researchers (Boršić et al. 2008) but this is expanded by the Croatian floristic online database, Flora Croatica (Nikolić 2015). The online list contains records for all of the aquatic aliens which have also been registered in Serbia, with *A. filiculoides* found mostly along its eastern border with Serbia and the presence of *E. nuttallii* registered at a single location in the far north-western corner of the country. However, it needs to be highlighted that both Anastasiu et al. (2007) and Flora Croatica (Nikolić 2015) consider *A. caroliniana* to be a synonym of *A. filiculoides*, which is in line with a classification proposed by Evrard and van Hove (2004) and the ITIS database (ITIS 2015). In conclusion, the number of registered aquatic aliens in Serbia, although not as high as in some European countries, is in line with other countries of the region. Due to the general lack of data on aquatic non-native plants in Serbia, this paper provides a valuable contribution to the existing knowledge base on aquatic aliens of Europe, their origins, current distribution, habitat preferences and invasiveness status.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Primary geo-referenced species record data for *Elodea canadensis* in Serbia.

Table S2. Primary geo-referenced species record data for *Elodea nuttallii* in Serbia.

Table S3. Primary geo-referenced species record data for *Azolla caroliniana* in Serbia.

Table S4. Primary geo-referenced species record data for *Azolla filiculoides* in Serbia.

Table S5. Primary geo-referenced species record data for *Vallisneria spiralis* in Serbia.

Table S6. Primary geo-referenced species record data for *Cabomba caroliniana* and *Paspalum distichum* in Serbia.

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